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Distribution of Active Ectomycorrhizal Short Roots in Forest Soils of the Inland Northwest: Effects of Site and Disturbance

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RESEARCH SUMMARY

An examination of the distribution of active ectomycorrhizal short roots among soil components of eight old-growth stands representative of the important timber growing lands of the Inland Northwest revealed a disproportionate concentration in surface organic materials. A similar concentration in the forest floor was present in six second-growth stands of various ages from the subalpine fir and Douglas-fir habitat series of western Montana. Exceptions to this trend were noted only in an extremely dry, old-growth, ponderosa pine stand and a highly disturbed site regenerating to a pure stand of young western larch. Even in these exceptional cases, ectomycorrhizal activities were concentrated in shallow mineral horizons relatively rich in organic materials. There was considerable variation in the quantity of soil organic materials on the 14 sites. In general, harsh and disturbed sites tended to have the least. The relative proportions of soil organic components (litter, humus, decayed wood) changed significantly both within and between sites. Distribution of active ectomycorrhizal short roots among those components during the early summer months was also significantly different, both within and between sites. Approximately 75 percent of active ectomycorrhizal short roots occurred in organic materials that represented only the first 4 cm of the soil depth. This disproportionate role of surface organic materials in supporting critical symbiotic processes emphasizes the need to carefully manage this important soil resource in forested ecosystems throughout the Inland West.

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INTRODUCTION

Recognition of the importance of symbiotic, ectomycorrhizal associations to survival and growth of forest trees (Vozzo and Hacskaylo 1971) has provided impetus for extensive research on conditions required to maintain this critical activity in forest soils. Soil conditions are of particular importance in altering the ability of ectomycorrhizal fungi and their hosts to start the association (Bjorkman 1970). Any forestry operation likely to alter soil conditions in a substantial way may change, perhaps reduce, the ability of soil to support ectomycorrhizal associations and attendant host growth. Because the fungi involved in ectomycorrhizal associations are obligatorily dependent on their host trees (Hacskaylo 1973), populations are reduced after harvest. Researchers have studied disturbance-caused changes of mycorrhizal populations (Danielson 1984) and reductions of mycorrhizal inoculum potential (Pilz and Perry 1984). Even in the relatively good soils of the Pacific Northwest, failure to initiate an adequate level of ectomycorrhizal activity can limit survival and performance of young conifers (Christy and others 1982; Trappe and Strand 1969).

Extensive examination of the distribution of forest tree feeder roots (Herman 1977) and ectomycorrhizal short roots (Fogel and Hunt 1979; Harvey and others in press; Meyer 1973; Mikola and others 1966; Vogt and others 1981) have shown that (1) they tend to occur at a shallow depth in the soil, and (2) they are usually associated with organic soil horizons, particularly in older stands (Fogel and Hunt 1979; Harvey and others 1976; Harvey and others in press; Vogt and others 1981).

Frequently the association of ectomycorrhizal activities with soil organic matter has specifically been with decayed wood (Harvey and others 1976, in press; McFee and Stone 1966; McMinn 1963; Trappe 1965). Decaying logs and soil wood are recognized as a unique ecosystem in Northwestern forests (Harvey and others in press; Maser and Trappe 1984) that represent an important source of nutrients and moisture (Barr 1930; Harvey and others 1978; Larsen and others 1980; Place 1950). Harvey and coworkers (1978, 1979) have shown that the distribution of ectomycorrhizal activities in decayed soil wood, as compared to the forest floor and mineral soil, changed with both season and site. Decayed wood supported relatively high mycorrhizal activity during dry seasons and on dry sites. The levels of decayed wood in the Inland Northwest may be affected by the trend toward greater use of harvesting residue, and this could have an impact on future site productivity (Jurgensen and others 1977).

The strong participation of the forest floor and shallow mineral horizons in nutrient cycling of many Inland Northwest forest ecosystems has led to concern regarding management (disturbance) of these important resources throughout the Inland West (Harvey and others in press). The purpose of this study was to investigate the involvement of surface soil components in ectomycorrhizal processes over (1) a wide range of mature ecosystems (habitat types) distributed throughout the Inland Northwest and (2) a range of site disturbance types within a local geographical area on similar habitat types.

STUDY SITES

A summary of site characteristics is provided in table 1.

Sample Sites, Old-Growth

Eight old-growth sites were chosen to be representative of a wide range of climatic and geographic conditions of the Inland Northwest, with emphasis on habitat series (Pfister and others 1977) most commonly associated with commercial forests. These sites had no history of human disturbance.

Site 1 (WH-M) is a western hemlock climax (habitat series) in northwestern Montana on the Coram Experimental Forest. It has a northwest aspect, a slope averaging 15 percent, and an elevation of approximately 1,000 m above mean sea level. The primary ectomycorrhizal host on this site is 250-year-old western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). Western larch (*Larix occidentalis* Nutt.) and western redcedar (*Thuja plicata* Donn.), the latter essentially a nonhost, also occur occasionally.

Table 1—A summary of site characteristics

Site number and acronym	Location	Aspect	Slope percent	Habitat series[1]	Dominant tree	Age	Treatment[2]
						Years	
1(WH-M)[3]	Western Montana	NW	15	Western hemlock	Western hemlock	250	Undisturbed
2(SAF-M)	Western Montana	E	55	Subalpine fir	Subalpine fir	250	Undisturbed
3(DF-M)	Western Montana	S	27	Douglas-fir	Douglas-fir	250	Undisturbed
4(WH-I)	Northern Idaho	E	5-15	Western hemlock	Western hemlock	250	Undisturbed
5(WWP-I)	Northern Idaho	NW	0-10	Western hemlock	Western white pine	250	Undisturbed
6(GF-I)	Northern Idaho	W	30-40	Grand fir	Western hemlock	250	Undisturbed
7(SAF-WY)	Northwestern Wyoming	N	15-25	Subalpine fir	Lodgepole pine	165	Undisturbed
8(PP-W)	Eastern Washington	W	15-35	Ponderosa pine	Ponderosa pine	200	Undisturbed
9(MIX-i)	Western Montana	E	40	Subalpine fir	Douglas-fir	80	WF
10(LPP-i)	Western Montana	W	5	Douglas-fir	Lodgepole pine	50	WF
11(WL-y)	Western Montana	N	10-20	Subalpine fir	Western larch	15-25	CC-BB
12(DF-i)	Western Montana	W	5-15	Douglas-fir	Douglas-fir	60-120	I-SC
13(PP-i)	Western Montana	SW	50-55	Douglas-fir	Ponderosa pine	80-100	PC-UB
14(LPP-y)	Western Montana	W	5	Subalpine fir	Lodgepole pine	15	WF

[1]Habitat series (Pfister and others 1977).
[2]Undisturbed = no history of human disturbance, WF = wildfire, CC-BB = clearcut-broadcast burn, I-SC = intermittent selective cut, PC-UB = partial cut with underburn.
[3]Beginning letters denote primary ectomycorrhizal host, last letters indicate State (caps) and age (lower case); i = intermediate age, y = young age.

Site 2 (SAF-WY) is a subalpine fir climax in northwestern Montana on the Coram Experimental Forest. It has an east aspect, a slope averaging 55 percent, and an elevation of approximately 1,900 m. The primary ectomycorrhizal hosts are 250-year-old Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western larch, subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and Engelmann spruce (*Picea engelmannii* Parry). Lodgepole pine (*Pinus contorta* Dougl.), western hemlock, and western white pine (*Pinus monticola* Dougl.) occur occasionally.

Site 3 (DF-M) is a Douglas-fir climax in northwestern Montana on the Coram Experimental Forest. It has a south aspect, a slope averaging 27 percent, and an elevation of approximately 1,150 m. The primary ectomycorrhizal host is 250-year-old Douglas-fir. Western larch occur infrequently on this site.

Site 4 (WH-I) is a western hemlock climax in northern Idaho near the Priest River Experimental Forest. It has an east aspect, a slope averaging 10 percent, and an elevation of approximately 1,500 m. The primary ectomycorrhizal host is 250-year-old western hemlock. Western redcedar occur frequently on this site.

Site 5 (WWP-I) is a western hemlock climax in northern Idaho on the Deception Creek Experimental Forest. It has a northwest aspect, a slope averaging 5 percent, and an elevation of approximately 1,000 m. The primary ectomycorrhizal host is 250-year-old western white pine. Western hemlock, Douglas-fir, and grand fir (*Abies grandis* [Dougl.] Lindl.) occur occasionally.

Site 6 (GF-I) is a grand fir climax in northern Idaho on the Priest River Experimental Forest. It has a west aspect, a slope averaging 35 percent, and an elevation of approximately 1,200 m. The primary ectomycorrhizal hosts are 250-year-old western hemlock and Douglas-fir. Western white pine, grand fir, and western redcedar occur occasionally.

Site 7 (SAF-W) is a subalpine fir climax in northwestern Wyoming near Union Pass. It has a north aspect, a slope

averaging 20 percent, and an elevation of approximately 2,800 m. The primary ectomycorrhizal host is 165-year-old lodgepole pine. Subalpine fir and Engelmann spruce occur occasionally.

Site 8 (PP-W) is a ponderosa pine climax located in northeastern Washington near Spokane. It has a west aspect, a slope averaging 25 percent, and an elevation of approximately 700 m. The only ectomycorrhizal host is 200-year-old ponderosa pine (*Pinus ponderosa* Laws.).

Sample Sites, Second-Growth

Three of the six disturbed sites were chosen to provide a uniform habitat series (subalpine fir climax type) from a localized geographic area representative of a common commercial forest in the Inland Northwest. The other three were chosen to provide a comparison with drier conditions (Douglas-fir climax type) from the same geographic area (western Montana). To represent a variety of harvesting and natural stand situations frequently found in the Inland Northwest, treatments (disturbance type) were chosen to provide a variation in time since disturbance and in species dominance.

Site 9 (MIX-i) (i = intermediate-aged) is a subalpine fir climax type in western Montana adjacent to the Hungry Horse Reservoir. It has an east aspect, a slope averaging 40 percent, and an elevation of approximately 1,500 m. This is an old wildfire-impacted site that now supports a mixed-species, pole-sized, 80-year-old stand of primarily Douglas-fir. Subalpine fir is also abundant. Western white pine, grand fir, and birch (*Betula papyrifera* Marsh) occur occasionally.

Site 10 (LPP-i) is a Douglas-fir climax type in western Montana near Martin City. It has a west aspect, a slope averaging 5 percent, and an elevation of approximately 1,200 m. This is an unharvested site with the previous stand terminated by wildfire. The present stand is 50 years old. The primary ectomycorrhizal host is lodgepole pine. Douglas-fir occurs occasionally.

Site 11 (WL-y) (y = young-aged) is a subalpine fir climax type in western Montana adjacent to the Coram Experimental Forest. It has a north aspect, a slope averaging 15 percent, and an elevation of approximately 1,300 m. This is a harvested site (clearcut and broadcast burned) with a planted, 15-year-old stand of western larch. The primary ectomycorrhizal species is western larch. No other hosts occurred within the plot.

Site 12 (DF-i) is a Douglas-fir climax type in western Montana on the University of Montana's Lubrecht Experimental Forest. It has a west aspect, a slope averaging 10 percent, and an elevation of approximately 1,200 m. The site has an extensive harvesting history (intermittent selective cutting) and now has a mixed-size, intermediate-aged stand (60 to 120 years old) of nearly pure Douglas-fir. The primary ectomycorrhizal species is Douglas-fir. No other host occurred within the sampled area.

Site 13 (PP-i) is a Douglas-fir climax type in western Montana adjacent to the Hungry Horse Reservoir. It has a southwest aspect, a slope averaging 50 percent, and an elevation of approximately 1,300 m. This harvested site (partial cut with an underburn) now has a residual stand of ponderosa pine, 80 to 100 years old. The primary ectomycorrhizal host is ponderosa pine. An occasional, small Douglas-fir occurred within the sampled area.

Site 14 (LPP-y) is a subalpine fir climax type in western Montana near the town of Hungry Horse. It has a west aspect, a slope averaging 5 percent, and an elevation of approximately 1,200 m. The previous stand originated as a result of wildfire in 1929. The stand was harvested by clearcut (with an occasional seed tree). At the time of sampling there was a 15-year-old regenerating stand of lodgepole pine. Lodgepole pine was the only ectomycorrhizal host, with no other hosts in the sampled area.

Climate

Thirteen of these sites are representative of the typical Inland Northwestern climate characterized by cold wet winters and warm dry summers. The weather on these sites is generated primarily by Pacific frontal systems. Site 7 is located on the east side of the Continental Divide so is more often impacted by continental weather, including frequent summer rainfall generated by thunderstorm activity.

STUDY METHODS

Individual soil samples consisted of 10- by 38-cm soil cores (Jurgensen and others 1977) taken randomly, five from around each plot center, 10 plot centers scattered evenly (approximately 30-m spacing) over 1 ha of uniform conditions on each of the 14 study sites. Conditions evaluated for uniformity included slope, aspect, soils, disturbance, stocking, and understory vegetation. Samples were taken during late spring and early summer over several years (1978 to 1982) to obtain maximum ectomycorrhizal activity for each site (Harvey and others 1978). Each soil core was subdivided in the field into the following components or horizons: litter (O_1 horizon); humus (O_2 horizon); brown cubicle decayed soil wood, also referred to as the O_3 horizon (Harvey and others 1979); surface mineral soil (the first 5 cm); and the remaining mineral soil to a depth of 30 cm. Each fraction was hand-separated and placed in a plastic bag immediately after collection. Volume and depth occupied by each fraction was determined by measuring its depth in the undisturbed core.

In the laboratory, each soil fraction was shaken for approximately 5 minutes in a standard 2-mm soil sieve. Decayed wood, humus, or mineral aggregates were gently crumbed before sieving. Soil and root material greater than 2 mm were thoroughly washed in running water and examined microscopically for ectomycorrhizal short roots.

Active ectomycorrhizal root tips were counted with the aid of a dissecting microscope (10-50×). Each active tip was counted, even though in many cases it was part of a complex structure. No attempt was made to count or differentiate between root tips that were inactive and those that were dead. The criteria used for identifying "active" ectomycorrhizal root tips have been described (Harvey and others 1976).

RESULTS

The total quantity of soil organic materials varied significantly between sites (table 2). In general, high-productivity, old-growth ecosystems had high organic reserves. Low-productivity, old-growth and second-growth ecosystems, particularly harsh ones, had low organic reserves. The percentage distribution of organic fractions (litter, humus, decayed wood) making up the organic mantle also varied significantly. There were usually substantial deposits of decayed wood in the forest floor on most sites.

The total number of active ectomycorrhizal short root tips also varied significantly between sites (table 3). As with soil organic matter, the high-productivity, old-growth stands had high numbers of active short root tips, and the low-productivity, disturbed second-growth stands, particularly harsh ones, had low numbers of active tips. There were many significant differences in percentage distribution of active ectomycorrhizal short root tips among the soil fractions, both within and between sites. The most striking general trends were reduced short root tips in the deep mineral fraction and high numbers in the organic fractions, particularly humus and decayed wood. Only two sites had the highest number of active short root tips in a mineral fraction: old-growth ponderosa pine (site 8) and a 15-year-old stand of western larch (site 11). In both cases it was the shallow (first 5 cm) mineral horizon that contained most of the active tips (table 3).

Soil wood as an ectomycorrhizal substratum is particularly interesting. A number of factors indicate that the association between decayed wood and mycorrhizal activities may be of importance to host trees. Todd (1979) reports ectomycorrhizal fungi on Douglas-fir may be able to break down certain organic materials directly, a means for closed-cycle nutrient turnover. Selective concentration of mycorrhizal inoculum in soil wood has been reported (Kropp and Trappe 1982; Trappe 1965, 1962). Roots of nonconiferous vegetation are seldom observed in soil wood (Berntsen 1955; Harvey and others in press; Rowe 1955). The apparent ability of mycorrhizal fungi to detoxify soil phenolics (Zak 1971) may contribute to the ability of conifer roots to thrive in decayed wood on and in forest soils. Thus, soil wood provides a relatively competition-free site for the growth of conifer feeder roots. In turn, this provides a decided advantage to the conifers because they are able to use this high-moisture material during drought (Harvey and others 1978) and on dry sites (Harvey and others 1979). Also, it is now apparent that some higher plants have hydrotropic roots (Jaffe and others 1985). Thus, the moisture contained in soil wood may be the primary reason for the concentration of conifer roots therein.

Although the number of samples taken on most of the sites was not sufficient to show significant differences in distribution of ectomycorrhizal activities among organic matter classes (table 4), the trend toward low numbers of short roots in the highest organic content class (> 45 percent of the core) was striking. This was particularly evident in moderate- to low-productivity, old-growth stands and in second-growth sites. This trend is likely related to soil moisture availability. Periodic rainfall on these sites may not be enough to wet deep organic matter deposits sufficiently to maintain them above the permanent wilting point, particularly during the normally dry growing

Table 2—Quantity and distribution of soil organic components from plots sampled

Site number and acronym	Total organic matter in soil core ($\bar{x}$ L/core)	Distribution of organic matter in forest floor: Litter	Humus	Decayed wood
	Liters	*Percent*		
Old-growth[1]				
1(WH-M)	[2]0.82[w]	[3]12[a]	38[b]	51[b]
2(SAF-M)	.77[w]	7[a]	45[b]	48[b]
4(WH-I)	.54[x]	12[a]	30[b]	58[b]
3(DF-M)	.50[x]	6[a]	58[b]	35[b]
5(WWP-I)	.43[x]	30[a]	19[b]	51[a]
8(PP-W)	.38[x]	31[a]	68[b]	2[c]
6(GF-I)	.32[y]	25[a]	61[b]	14[a]
7(SAF-WY)	.15[z]	34[a]	52[b]	14[a]
Second-growth				
10(LPP-i)	.42[x]	19[a]	58[b]	23[a]
9(MIX-i)	.39[x]	19[a]	46[b]	36[ab]
11(WL-y)	.32[x]	21[a]	41[b]	39[ab]
12(DF-i)	.26[x]	22[a]	42[b]	35[ab]
13(PP-i)	.12[z]	27[a]	58[b]	15[a]
14(LPP-y)	.12[z]	46[a]	40[a]	14[b]

[1]See table 1 for explanation of abbreviations.
[2]Average includes all organic matter-containing strata. Differing letters indicate significant differences down column (w-z), α = 0.05, ANOVA, Duncan's multiple range test.
[3]Differing letters (a-c) indicate significant differences (α = 0.05) within treatments, between individual strata, detected by two-sided t-test on actual volume measurements.

Table 3—Number and distribution of active ectomycorrhizal root tips in soil strata; all samples taken during June to July peak activity period (Harvey and others 1978)

Site number and acronym	Number ectomycorrhizal roots ($\bar{x}$) all strata combined	Percent distribution of ectomycorrhizal root tips in				
		Litter	Humus	Decayed wood	Shallow mineral	Deep mineral
	No./liter			*Percent*		
Old-growth[1]						
5(WWP-I)	[2]120^{w}	[3]10^{ab}	57^{b}	26^{ab}	6^{c}	1^{d}
4(WH-I)	95^{wx}	6^{acde}	67^{b}	16^{cd}	8^{d}	3^{e}
1(WH-M)	93^{wx}	6^{a}	32^{b}	51^{bc}	10^{ac}	1^{a}
7(SAF-WY)	65^{x}	6^{a}	37^{b}	28^{a}	28^{a}	1^{a}
8(PP-W)	60^{x}	1^{a}	8^{ac}	7^{ac}	74^{b}	10^{c}
2(SAF-M)	21^{y}	0	74^{a}	19^{bc}	6^{b}	1^{c}
6(GF-I)	14^{y}	26^{a}	13^{a}	31^{a}	20^{a}	10^{a}
3(DF-M)	11^{y}	14^{a}	30^{a}	31^{a}	21^{a}	2^{b}
Second-growth						
9(MIX-i)	49^{x}	6^{ac}	47^{b}	35^{abc}	10^{c}	2^{a}
10(LPP-i)	41^{x}	10^{ab}	15^{a}	57^{ab}	15^{a}	2^{b}
13(PP-i)	29^{x}	0	25^{a}	61^{a}	11^{a}	2^{b}
14(LPP-y)	14^{y}	0	36^{a}	40^{a}	21^{a}	3^{b}
11(WL-y)	7^{z}	1^{a}	23^{a}	7^{ab}	57^{c}	11^{b}
12(DF-i)	4^{z}	20^{a}	0	46^{a}	33^{a}	1^{b}

[1]See table 1 for explanation of abbreviations.
[2]Differing letters indicate significant differences (α = 0.05) between sites, down column (w-z), and within strata and site, across (a-e), based on two-sided t-test of numbers of short root tips/liter.
[3]Ectomycorrhizal distribution in individual strata shown as a percentage of the total to facilitate between site comparisons.

seasons. Also, many sites with limited organic matter production have few substantial deposits accumulated, and those that do are likely to be disrupted by harvesting-related disturbances and natural wildfires. These results appear to support a management recommendation to maintain 2.4-3.6 tons/ha (10-15 tons/acre) (based on the 31 to 45 percent volume class) of woody residues to maintain soil organic reserves (Harvey and others 1981).

The concentration of ectomycorrhizal short root tips in shallow organic horizons (table 5) makes them extremely vulnerable to external perturbation. Even moderate physical disturbance or heating is likely to produce high mortality of short roots from nearby trees. Also, because it is now apparent that moisture laden with air pollutants (acid rain) can inhibit ectomycorrhizal activities (Reich and others 1985), their concentration in shallow horizons of Inland West forests may make them extremely vulnerable to air pollution damage. A shallow distribution of feeder roots from conifers has been noted (Fogel and Hunt 1979; Maser and Trappe 1984; Mikola and others 1966; Vogt and others 1981).

In the two instances reported here where the most ectomycorrhizal short root tips were not concentrated in the organic horizons (table 5, sites 8—old-growth ponderosa pine—and 11—second-growth western larch), they were concentrated in the topmost mineral layer (table 4). In one of these instances the dominant host (ponderosa pine) is a relatively deep-rooted species (Steinbrenner and Rediske 1964) growing on an extremely dry site where surface moisture is episodic and rare during the growing season. In the other instance, the dominant host was young western larch, a well-adapted pioneer species growing on a highly disturbed site with little surface organic matter present.

When soil organic matter content was grouped into volume classes for each site, numbers of active short root tips compared between classes showed no significant differences in distribution (table 4). However, a strong trend toward low numbers in the highest organic matter class (> 45 percent of the core) was evident. Also evident was the low percentage volume of the cores represented by organic fractions in all but the most productive ecosystems (table 2, table 4). When the comparison between organic classes was made on a larger sample base (150 cores), significant differences between classes within the Coram Experimental Forest sites in Montana for old-growth western hemlock, subalpine fir, and Douglas-fir (sites 1, 2, 3) were found (table 4).

A comparison of the distribution of ectomycorrhizal short root tips in all organic versus all mineral soil fractions (combined) showed a strong, frequently significant trend favoring organic fractions for all but the old-growth ponderosa pine and second-growth western larch sites (sites 8, 11) (table 5). A direct measurement of the depth of organic horizons (litter, humus, and decayed wood combined) showed the extreme shallow nature of organic

Table 4—Distribution of active ectomycorrhizal root tips (percentage of total in core) among organic matter (litter, humus, decayed wood) volume classes within and between sites; all samples taken during June to July peak activity period (Harvey and others 1978)

Site number and acronym	Mean percent of core organic	Organic matter volume class (percent)			
		0-15	16-30	31-45	>45
		Percent			
Old-growth[1]					
1(WH-M)	31	[2]13[a]	45[b]	23[c]	19[d]
2(SAF-M)	30	12[a]	57[b]	27[b]	5[a]
4(WH-I)	28	20	49	21	10
3(DF-M)	19	7[a]	36[b]	52[b]	4[c]
5(WWP-I)	17	12	20	40	27
8(PP-W)	15	39	44	17	0
6(GF-I)	13	44	43	13	0
7(SAF-WY)	6	58	0	42	0
Second-growth					
10(LPP-i)	17	57	12	31	0
9(MIX-i)	17	42	36	22	0
11(WL-y)	13	57	20	22	0
12(DF-i)	12	0	100	0	0
13(PP-i)	5	39	44	17	0
14(LPP-y)	5	100	0	0	0

[1]See table 1 for explanation of abbreviations.
[2]Within the sample used for these calculations (50 cores) no significant differences between treatments could be detected. However, on the three sites for which a larger sample was available (150 cores, Harvey and others 1981) significant differences were detected within the three sites (α = 0.05), two-sided t-test, differing letters indicate significant differences.

Table 5—Cumulative depth (centimeters) of organic soil strata and distribution of active ectomycorrhizal short roots in organic and mineral strata within and between sites; all samples taken during June to July peak activity period (Harvey and others 1978)

Site number and acronym	Cumulative depth/core of organic horizons	Total ectomycorrhizal short root tips in	
		Organic horizons (all)	Mineral horizons (all)
	cm	*Percent*	
Old-growth[1]			
1(WH-M)	3.8	[2]89[a]	11[b]
2(SAF-M)	3.5	93[a]	7[b]
4(WH-I)	2.5	89[a]	11[b]
3(DF-M)	2.3	76[a]	24[a]
5(WWP-I)	2.0	93[a]	7[b]
8(PP-W)	1.7	16[a]	84[b]
6(GF-I)	1.5	70[a]	30[a]
7(SAF-WY)	.7	71[a]	29[a]
Second-growth			
10(LPP-i)	1.9	82[a]	18[a]
9(MIX-i)	1.8	89[a]	11[a]
11(WL-y)	1.5	31[a]	69[b]
12(DF-i)	1.2	66[a]	34[a]
13(PP-i)	.6	86[a]	14[a]
14(LPP-y)	.5	76[a]	24[a]

[1]See table 1 for explanation of abbreviations.
[2]Differing letters indicate significant differences (α = 0.05) within site, based on two-sided t-test of numbers of short root tips in combined strata.

horizons (less than 4 cm) in these forests, particularly low-productivity, harsh, or disturbed sites (table 5). The same trend was shown for percentage of the core (table 4) and total volume of sample (table 2) represented by organic horizons.

DISCUSSION

The tendency to accumulate soil organic matter in the mature, productive stands studied is probably a simple reflection of biomass production (table 2). However, the significantly greater accumulation on the western hemlock and subalpine fir sites in western Montana (sites 1 and 2) as compared to the western hemlock, white pine, and grand fir sites in northern Idaho that have higher productivity (sites 4, 5, 6—Pfister and others 1977) may indicate that the cool Montana climate slows decay of organic residues enough to offset higher biomass production in Idaho. The thin organic horizons on low to moderate productivity habitat series are commensurate with their production. The low to extremely low organic reserves (organic component volume by depth) on the variously disturbed sites likely reflect mixing, transport, and loss of the forest floor due to harvesting and site preparation (tables 2 and 5).

The distribution of soil organic components was highly variable in both combined total and individual quantity (table 2). However, substantial reserves of decayed wood were present in most of the old-growth stands, except those likely to have a frequent fire history (sites 6, 7, 8). Similarly, substantial reserves of decayed wood were present in most second-growth sites except where site preparation had been extensive (sites 13, 14). The relatively good balance between the long-lived organic components (wood and humus) on most of these sites may result from a usually infrequent or low-temperature fire history that allows production of the large woody residues required to produce soil-wood deposits.

Numbers of ectomycorrhizal short root tips also generally reflected site productivity, particularly of the undisturbed stands. On the second-growth sites, short root tip numbers were moderate in intermediate-aged stands and low in young stands (table 3). These numbers likely reflect the root density of host trees. However, reduced organic horizons may also be a contributing factor. Organic materials contain most of the soil nutrients (Harvey and others in press) and moisture (Barr 1930; Harvey and others 1978; Place 1950) and are a highly favorable substrate for ectomycorrhizal activities (Fogel and Hunt 1979; Harvey and others 1976, 1979, in press; Maser and Trappe 1984; Mikola and others 1966; Vogt and others 1981).

The highly significant distribution patterns of active ectomycorrhizal short root tips among the various soil components, both within and between sites (table 3), are likely brought about by the individual nature of these components as conditioned by the climate and fertility of the site (Harvey and others in press). For example, humus is an attractive substrate for feeder roots because of its high nutrient content, but its shallow depth limits moisture retention. On the other hand, soil wood is moderately supplied with nutrients but usually occurs in large enough volumes to be a significant source for moisture.

CONCLUSION AND APPLICATIONS

Perhaps the most striking effect (or lack thereof) of site or disturbance on numbers of ectomycorrhizal root tips, including differences in host species and time (age), was the generally similar distribution of ectomycorrhizal roots among organic versus mineral soil horizons. In most cases short root tips were concentrated in organic horizons. On the two sites where this did not occur, the forest floor was thin and root tips were most numerous in the surface mineral layer. Thus, the surface soils, particularly the organic horizons, were universally important for supporting this important feeder root activity on all 14 sites. This is a clear indication that management methods likely to impact soil surfaces, particularly mechanical site preparation and broadcast burning, should be applied with caution to minimize loss or disruption of surface soil horizons, organic and mineral. The extremely shallow distribution of most ectomycorrhizal activity (4 cm or less) emphasizes a critical need to protect this valuable resource.

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Approximately 75 percent of ectomycorrhizal activities that occurred in soils from eight undisturbed and six variously disturbed sites occurred in shallow organic horizons. These horizons represented only the first 4 cm of soil depth. This disproportionate participation of surface organic materials emphasizes a need to conserve them in forested ecosystems of the Inland West.

KEYWORDS: soil microbial activity, soil quality, soil productivity, soil management, fire management, site preparation, site protection

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